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The development of prothallia and antheridia from the sex organs of Polypodium irioides

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(WITH PLATE 4 AND FOUR TEXT FIGURES)

INTRODUCTION

The spores of *Polypodium irioides* Poir., from the culture of which were obtained the prothallia with the sex-organs to be described, were sown March 21, 1916. When the first prothallia had grown to maturity and a number had already produced sporophytes, the majority were removed for class use. Antheridia and archegonia were formed on the prothallia in large numbers. The archegonia, as is usual in most ferns, were produced on the cushion back of the apical notch, and the antheridia in the majority of cases on the posterior portion among the rhizoids. They were also frequently formed along the margins of the prothallia. In a few instances antheridia were observed among the archegonia.

On several occasions prothallia were examined with the microscope, but no abnormalities were observed in the development of the sex-organs. The smaller prothallia, as well as the larger ones, produced secondary prothallia in profusion. A modified Beyerinck's solution* was several times applied to the *Sphagnum* on which the prothallia were grown. The illumination and the carbon dioxide and oxygen supply were sufficient for normal development of prothallia. The vigorous growth and the large size of the prothallia suggest that favorable conditions prevailed in the culture at least during its early history.

The majority of the remaining prothallia were removed in October, 1918. Three sporophytes remained in the culture at this time and from these sporophytes sporophytic and aposporous

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*See Moore, G. T. Methods for growing pure cultures of Algae. Jour. Appl. Microscopy **6**: 2309–2314. 1903.

growths were later produced. For a description of these the reader is referred to another paper.*

The figures made as a result of this investigation were drawn with the aid of a camera lucida from living material. Some of the prothallia with the abnormal archegonia were fixed in Flemming's medium fluid, imbedded in paraffin, sectioned and finally stained with safranin and light green.

ANTHERIDIA

In the autumn of 1918, when the first sporophytes were observed to produce secondary sporophytes, the antheridia and archegonia to be described were discovered.

The majority of the antheridia appeared normal at this time, producing actively motile antherozoids. When these sex-organs were mature, the sterile cells contained only a few chloroplasts. A large number of abnormal antheridia developed among the normal ones. The lid cell and the two ring cells of the abnormal type of antheridium contained usually a large number of chloroplasts. Such antheridia were primarily vegetative in character and only occasionally produced mature antherozoids. These antheridia were not confined to the older prothallia, but were most frequently found on the younger filaments or secondary prothallia, which (as has already been stated) were commonly developed in the culture after some of the larger prothallia were removed.

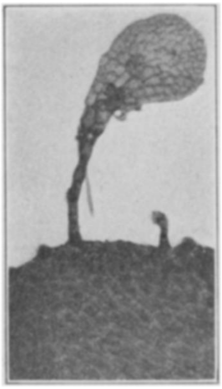

FIG. 1. A portion of a prothallium of *Polypodium irioides* from which a filament was produced. An antheridium at the end of the filament developed a prothallium. × 20.

From the sterile cells of these antheridia prothallial filaments or secondary antheridia were frequently produced. The most common cases of regeneration were observed in connection with the lid cell. Such filaments always consisted of a single row of cells. Early stages in the development of the filaments are represented in FIGS. 1 and 2 of PLATE 4. These filaments were observed to broaden out in some instances and form heart-shaped prothallia with rhizoids and antheridia. (TEXT FIG. 1.) The antherozoids produced in the antheridia were seldom discharged in these instances and undoubtedly disintegrated. One of the ring cells of the antheridium represented by FIG. 2 developed a secondary antheridium from which the antherozoids had already escaped.

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* Steil, W. N. Vegetative reproduction and aposporous growths from the young sporophyte of *Polypodium irioides*. Bull. Torrey Club 48: 203–205. *f. 1–3.* 1921.

In many instances, the sterile cells of an antheridium produced secondary antheridia. Sometimes several of these were developed from the lid cell. FIG. 3 represents a lid cell (*a*) from which an antheridium (*b*) was produced. From the lid cell (*d*) of the larger secondary antheridium (*c*) a normal one (*e*) was developed. Occasionally a ring cell produced one or more antheridia (FIGS. 4–6).

The spermatogenous cells in antheridia whose sterile cells contained many chloroplasts, in several instances were observed to have disintegrated. Such antheridia were sometimes transformed into prothallia (FIGS. 7–9). The cells of such antheridia usually increased in size and often divided into a number of cells (FIG. 10). The great difference between normal and such abnormal antheridia is shown by FIG. 9. Many-celled prothallia produced from this kind of antheridium were found in the culture.

Antheridia were also transformed into prothallia during their early course of development. It was obviously difficult to follow the development of these prothallia. An early stage in the transformation of an antheridium is shown by FIG. 11. The ring cells, in this instance, had divided to produce several cells. In some cases plastids were present in the central portion of the antheridium. These were, however, almost colorless, containing little chlorophyl. In this respect the young prothallia of this type differed from the ordinary secondary prothallia. The development of these prothallia could be followed only during their early stages, since at later stages of development they became similar in all respects to secondary prothallia produced in the culture. A most convincing instance of the transformation of an antheridium is represented by FIG. 12. The antherozoid cells can still be distinguished. The sterile cells by a number of divisions have produced a small prothallium which has already formed a rhizoid.

A number of antheridia were observed in which there was an unusual number of cells as is represented by FIG. 13. The lower portion (*a*) of this antheridium is peculiar since there was present an additional ring cell.

ARCHEGONIA

The frequent occurrence of secondary prothallia among the archegonia suggested that some of them may have originated from these sex-organs. By a careful examination of the prothallia, this idea was confirmed. Frequently prothallial filaments were produced from the neck and the venter cells, especially from the latter. FIG. 14 represents a filament of a number of cells which has arisen from a single neck cell. An early stage in the development of a prothallium from a venter cell is represented by TEXT FIG. 2. The archegonium which had opened in this instance bore an egg (*e*) which had disintegrated. The filaments produced from the archegonia often grew to a considerable length and invariably developed numerous antheridia (TEXT FIG. 3). Frequently plates of cells instead of prothallial filaments were developed from the archegonia (FIGS. 15 and 17).

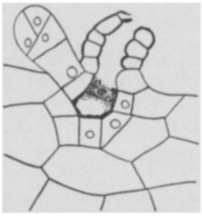

FIG. 2. A section of a young prothallium of *Polypodium irioides* produced from the venter of an archegonium. × 200.

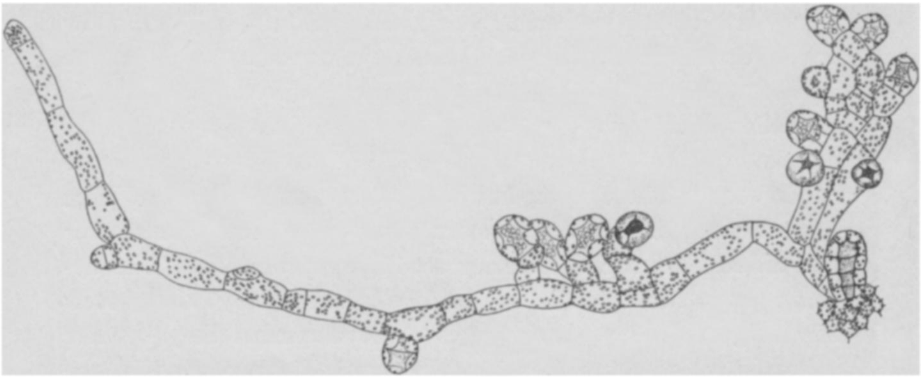

FIG. 3. Regeneration from the venter of anarchegonium of *Polypodium irioide.* Numerous antheridia have been produced by the prothallial filaments. × 100.

From the neck cells of these abnormal archegonia antheridia were also produced. Such antheridia were normal in development (FIGS. 15 and 16). The antheridia thus produced also developed secondary ones (FIG. 16, *b*).

The archegonia at no time were found to develop secondary archegonia. The transformation of archegonia into prothallia was never observed. In these two respects the archegonia differed in behavior from the antheridia.

The archegonia with the behavior just described were like the antheridia, vegetative in nature, numerous chloroplasts being present in the sterile cells. The axial row of cells of the archegonia from which regeneration occurred frequently disintegrated before the archegonia opened. Such a stage is represented by TEXT FIG. 4. It will be observed that some of the neck cells in this case have already divided (*a*, *c*).

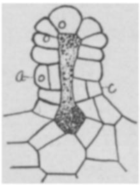

FIG. 4. An archegonium of *Polypodium irioides* in which the axial row of cells has disintegrated. Dividing cells at *a* and *c*. × 200.

CULTURAL CONDITIONS

It is impossible to state under what cultural conditions the sex-organs of *Polypodium irioides* regenerated in the manner described. Since no abnormalities appeared in the early history of the culture, it is probable that the peculiar behavior of the antheridia and the archegonia was the result of unfavorable conditions which appeared in the old culture.

DISCUSSION

No case of regeneration from the sex-organs of a pteridophyte has been previously reported. In the mosses Correns* and Collins† (1919) described the formation of protonemata from the antheridia of *Funaria hygrometrica* (L.) Schreb. Miss Brown‡ found in the same species that protonemata could be induced to form also from the archegonia. In no instance, however, has the formation of antheridia been observed from *either* sex-organ of *any bryophyte.*

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* Correns, Carl. Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge. Jena. 1899.

† Collins, E. J. Sex segregation in the Bryophyta. Jour. Genetics **8**: 139–146. 1919.

‡ Brown, Mabel Mary. Unpublished paper.

SUMMARY

In an old culture of prothallia of *Polypodium irioides*, the sterile cells of a large number of antheridia and archegonia became vegetative like ordinary prothallial cells.

The lid and the ring cells of the antheridia produced prothallial filaments and secondary antheridia.

The archegonia produced similarly from the neck and the venter cells filaments and antheridia, but in no case secondary archegonia.

At some time during their course of development, antheridia were transformed into prothallia. No such transformations were observed to occur among the archegonia.

The prothallia produced from the sex-organs resembled those formed from the germination of a spore.

Secondary antheridia arising from antheridia and archegonia developed actively motile antherozoids.

Unusual cultural conditions probably diverted the sex-organs of *Polypodium irioides* from their normal course of development.

No similar case of regeneration has been previously reported in a *pteridophyte*.

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Explanation of plate 4

FIG. 1. Antheridia of *Polypodium irioides* Poir.; the lower one with a vegetative ring cell, the upper one with a prothallial filament of two cells produced by a ring cell. × 200.

FIG. 2. An antheridium from the lid cell of which has been produced a filament of four cells. The upper ring cell with a secondary antheridium from which the antherozoids have escaped. × 200.

FIG. 3. The lid cell (*a*) of an antheridium has formed two antheridia (*b* and *c*) from the lid cell of the latter of which another antheridium has been produced. × 230

FIG. 4. Two secondary antheridia produced from a single ring cell of an antheridium. × 230.

FIG. 5. An antheridium-like structure produced from the upper ring cell. × 230.

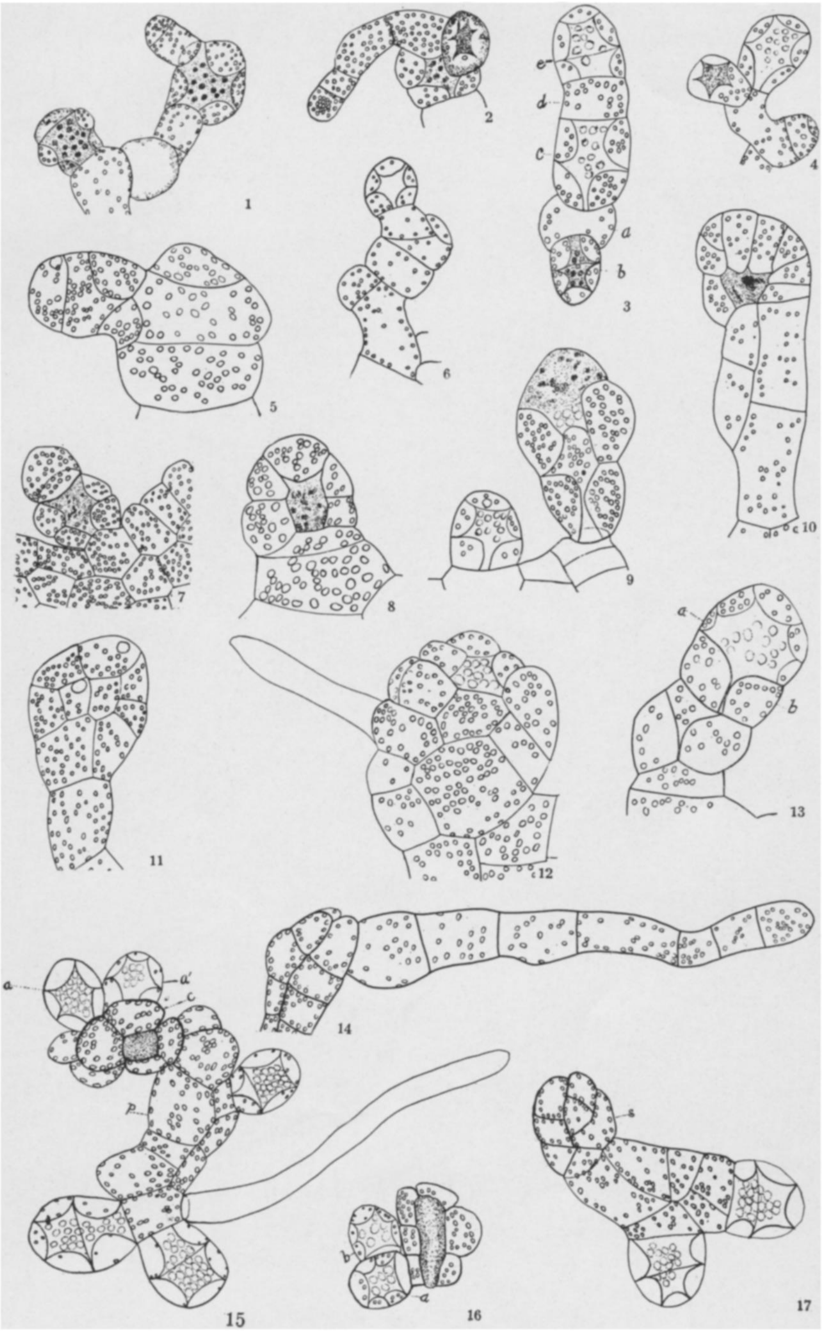
FIG. 6. The upper ring cell has divided and from one of the cells another antheridium has been developed. × 200.

FIG. 7. An antheridium whose central cells have disintegrated. The sterile cells contain numerous chloroplasts. × 200.

FIG. 8. An antheridium similar to the above. × 393½.

FIG. 9. A normal (*a*) and an abnormal (*b*) antheridium. The upper portion of the latter is disintegrating. × 393½.

FIG. 10. A stage in the transformation of an antheridium into a prothallium. × 200.



STEIL : POLYPODIUM IRIOIDES

FIG. 11. A young prothallium produced by the transformation of an antheridium. × 200.

FIG. 12. A small prothallium similar to above. Antherozoids present. × 200.

FIG. 13. An antheridium with three ring cells. × 200.

FIG. 14. A prothallial filament formed from the neck of an archegonium. × 230.

FIG. 15. Antheridia and a small prothallium produced from the neck of an archegonium. × 200.

FIG. 16. An antheridium (*a*) developed from the neck of an archegonium. From this antheridium a secondary antheridium (*b*) has been formed. × 200.

FIG. 17. A plate of cells produced from the neck of an archegonium. Two normal antheridia have been formed from the prothallial plate. × 200.